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ATTACK BY BARK BEETLES (COLEOPTERA: SCOLYTIDAE) FOLLOWING SPACING OF MATURE LODGEPOLE PINE (PINACEAE) STANDS

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Abstract

Variation in bark beetle attack following spacing of mature lodgepole pine stands in the East Kootenays of British Columbia was analyzed in relation to stand location (site), spacing treatment, and harvesting injury. Observations were made on three sites, each having three treatments: 4 × 4 m spacing, 5 × 5 m spacing, and untreated control. There was no statistically significant difference in the numbers of attacked trees among sites or treatments. However, in the spaced plots 94.3% of the attacked trees sustained harvesting injury or were located adjacent to skid trails. *Dendroctonus valens* LeConte was the dominant species attacking trees on the two drier sites, and *Dendroctonus murrayanae* Hopkins was the dominant species on the third site. There was no statistically significant variation in the percentage of attacked stumps among sites or spacing treatments. On average, 80.7% of the stumps were attacked; attacked stumps had larger diameters than unattacked stumps. Thirteen species of bark beetles were found attacking stumps. *Hylurgops porosus* LeConte was the most numerous species at all three sites. Based on the fit of the Michaelis–Menten equations to species accumulation curves, an estimated 76–90% of the number of species attacking stumps at the three sites were observed in bark samples. Margalef's index of diversity for the two drier sites (Cranbrook = 1.15, Parson = 1.13) was nearly identical and higher than at the moist site (Elkford = 0.89). Pairs of sites had five to six species in common, and the Sorensen coefficient of similarity ranged from 0.52 to 0.71, indicating moderate similarity in species composition. The abundance *versus* species rank relationship was fitted by three models: the MacArthur broken stick model, the geometric series, and the Zeta distribution. The latter gave good fit to data from two sites, but none of the fitted models gave satisfactory fit to data from the third site, mainly because of the high abundance of the second ranked species (*Orthotomicus caelatus* Eichhoff). Our results indicated that stand characteristics affected species assemblages and abundances of bark beetle species that attacked stumps. Management practices that minimize injury to trees during the spacing operations are emphasized to reduce attack by bark beetles.

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Résumé

Dans des peuplements mûrs de pin tordu latifolié des monts East Kootenay, en Colombie-Britannique, nous avons analysé les différences de taux d'infestation par les scolytes à la suite d'une éclaircie, selon la position du peuplement (station), le taux d'éclaircie et les blessures subies par les arbres. Dans chacune des trois stations étudiées, trois traitements d'éclaircie ont été effectués : éclaircie 4 × 4 m, éclaircie 5 × 5 m et absence d'éclaircie (témoin). Nous n'avons observé aucune différence significative entre les stations ni entre les traitements quant au nombre de souches infestées. Cependant, dans les parcelles éclaircies, 94,3% des arbres infestés avaient subi des blessures durant la récolte ou étaient situés à proximité de chemins de débardage. Le *Dendroctonus valens* LeConte était l'espèce dominante parmi les scolytes

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infestant les arbres des deux stations les plus sèches, tandis que le *Dendroctonus murrayanae* Hopkins dominait dans la troisième station. De même, nous n'avons relevé aucune différence significative entre les stations ni entre les traitements quant au pourcentage de souches infestées. Ce pourcentage était de 80,7% en moyenne, et les souches infestées avaient un plus fort diamètre que les souches non infestées. Dans les souches infestées, nous avons relevé 13 espèces de scolytes. Dans les trois stations, l'espèce la plus abondante était l'*Hylurgops porosus* LeConte. En ajustant les équations de Michaelis–Menten aux courbes cumulatives d'espèces, nous avons pu estimer que les espèces observées dans les échantillons d'écorce représentaient 76 à 90% des espèces infestant les souches dans les trois stations. Par ailleurs, l'indice de diversité de Margalef était à peu près identique dans les deux stations les plus sèches (1,15 à Cranbrook et 1,13 à Parson), alors qu'il était moins élevé dans la station la plus humide (Elkford, 0,89). Chaque paire de stations présentait cinq ou six espèces en commun, et les compositions en espèces présentaient une similarité modérée, puisque les coefficients de similarité de Sorensen allaient de 0,52 à 0,71. La relation entre l'abondance et le rang de chaque espèce a été ajustée selon trois modèles : le modèle du bâton brisé de MacArthur, la série géométrique et la distribution zêta. Ce dernier modèle permettait un bon ajustement des données provenant de deux des stations, mais aucun des modèles ne permettait un ajustement satisfaisant des données de la troisième station, principalement à cause de l'abondance élevée de l'espèce occupant le deuxième rang, l'*Orthotomicus caelatus* Eichhoff. Ces résultats montrent que les caractéristiques stationnelles ont un effet sur les scolytes s'attaquant aux souches, quant aux espèces présentes et à l'abondance de chacune. Pour réduire les risques d'infestation par les scolytes, il faut donc privilégier les pratiques d'aménagement qui causent le mois de blessures aux arbres durant l'éclaircie.

Introduction

Manipulation of stand density is one of the most important tools available to foresters to achieve a broad range of goals, including insect and disease management (Ramsey 1998). Thinning mature lodgepole pine, *Pinus contorta* var. *latifolia* Engelm. (Pinaceae), stands to alter within-stand climate and improve or maintain tree vigour has shown promise in reducing susceptibility to attack by mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) (Amman 1989; Mitchell *et al.* 1983; Waring and Pitman 1985). Late thinning may also be used to encourage natural regeneration (where minor components of other species are present in the stand), or to protect underplanted seedlings in a shelterwood silvicultural system. A resulting mixed species stand, taken to rotation with stocking control and species discrimination, would be less susceptible to beetle attack (Cole and McGregor 1985) and could provide flexibility and diversity for future products and integrated resource management objectives. Silvicultural thinning, however, leaves a large number of stumps, and heavy machinery used during the operation may injure the remaining trees by compacting soil and damaging root systems and by bark removal from abrasion or collision. Stumps and injured trees are normally attacked by a number of bark beetle species. The effects of thinning on infestation incidence and species interactions by bark beetles in mature lodgepole pine are unknown.

This paper describes the characteristics of bark beetle attacks on the residual trees and stumps for the first 3 years after spacing mature lodgepole pine stands. The species richness and abundance *versus* species rank relationship for bark beetle species that attacked stumps was also analyzed.

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TABLE 1. Means (SE) of tree density, diameter at breast height (DBH), and tree height by treatment and site for the study areas in British Columbia.

Spacing	Sample size*	Density (no. of trees/ha)	DBH (cm)	Height (m)
		Cranbrook		
Control	18	1902.2 (242.2)	16.3 (0.7)	20.9 (0.3)
4 × 4 m	18	503.8 (35.4)	21.6 (0.7)	21.4 (0.2)
5 × 5 m	18	434.4 (53.8)	18.7 (0.5)	20.6 (0.2)
		Elkford		
Control	18	1223.6 (111.0)	21.0 (0.8)	24.3 (0.3)
4 × 4 m	18	697.5 (95.3)	22.4 (1.2)	23.4 (0.2)
5 × 5 m	18	443.3 (71.7)	25.4 (2.0)	25.3 (0.3)
		Parson		
Control	18	1002.8 (153.9)	20.2 (1.2)	24.3 (0.3)
4 × 4 m	18	588.7 (55.3)	19.5 (0.5)	24.1 (0.3)
5 × 5 m	18	406.3 (79.5)	21.9 (1.2)	24.6 (0.3)

NOTE: Density and DBH data were collected on prism plots centred on the corners of the nine interior subplots of each of two 1-ha plots (macroplots) per spacing treatment. Height data were based on 20 randomly selected trees per macroplot.

*Average tree heights were based on samples of 40 trees.

TABLE 2. The percentage of tree species by site in British Columbia.

Tree species	Cranbrook	Elkford	Parson
Pinus contorta	94.2	74.1	90.7
Picea hybrids	0.7	18.8	1.0
Larix occidentalis	4.5	0	0
Pseudotsuga menziesii	0	0.7	8.0
Abies lasiocarpa	0	6.4	0.3
Deciduous species	0.6	0	0
Total	100	100	100

NOTE: Two 25 × 25 m subplots were sampled within each of two 1-ha plots per spacing treatment.

Methods

Stand Description and Field Procedures. Three areas in the East Kootenays of British Columbia were selected in the summer of 1992: (1) 14 km north of Elkford (50°01′N, 114°55′W), (2) 10 km southeast of Cranbrook (49°30′N, 115°46′W), and (3) 10 km southwest of Parson (51°4′N, 116°38′W). The forest at each location consisted of uniform lodgepole pine dominated stands, 80–100 years of age (Tables 1, 2). The stands at Elkford and Cranbrook were harvested during the winter of 1992–1993, and the stand at Parson was harvested during the winter of 1993–1994.

The Cranbrook area is located on the Haha Creek Forestry Road at an elevation of 1340 m. This area is in the MSdk-04 site series (lodgepole pine – Oregon grape *Mahonia nervosa* (Pursh) Nutt. (Berberidaceae) – pine grass *Calamagrostis rubescens* Buckley (Poaceae) site series of the Dry Cool Montane Spruce Subzone) in the biogeoclimatic classification (Braumandl and Curran 1992). The stands consist of mature lodgepole pine with a few western larch, *Larix occidentalis* Nutt., hybrid spruce, *Picea*

glauca (Moench) Voss × *Picea engelmannii* Parry, Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and subalpine fir, *Abies lasiocarpa* (Hook.) Nutt. (Pinaceae).

The Elkford area is located north of the town of Elkford in the Bingay Creek area at 1450 m elevation. The stand is on an easterly facing slope and lodgepole pine is the dominant tree species, but hybrid spruce, subalpine fir, and western white pine, *Pinus monticola* Douglas, are conspicuous. This area is ecotonal between the ESSFdk and the MSdk subzones (Braumandl and Curran 1992).

The Parson area is located on a river terrace southwest of the town of Parson at an elevation of 1100 m. Lodgepole pine is dominant, with a few Douglas-fir, hybrid spruce, and subalpine fir present. The site series is mostly hybrid spruce – soopolallie *Sheperdia candensis* (L.) Nutt. (Elaeagnaceae) – grouseberry *Vaccinium scoparium* Leiberg (Ericaceae) (MSdk-01 site series)(Braumandl and Curran 1992).

The thinning treatments were laid out in a randomized complete block design in the three blocks (Cranbrook, Elkford, and Parson). Within each block four main plots were established, each consisting of two 1-ha (100 × 100 m) macroplots. The macroplots were further divided into 25 × 25 m subplots. The main plots and macroplots within them were surrounded and separated by 25- to 75-m buffer zones. One of the following treatments was assigned to each main plot: (1) 4.0 × 4.0 m spacing, (2) 5.0 × 5.0 m spacing, and (3) control (no spacing).

The spacing prescription called for retention of dominant and codominant trees, free from visible defect, with as uniform intertree spacing as possible. Trees to be retained within the plots were marked during the summer of 1992. At Cranbrook and Parson, feller-bunchers were used for harvesting and skidding, whereas at Elkford trees were hand-felled and skidded with a crawler tractor or a wheeled skidder. The logistics of the harvesting operations at Cranbrook and Elkford have been described by Mitchell (1994).

Tree diameter at breast height (DBH, 1.3 m), height, and stand density were determined prior to and following the spacing operation using prism plots centred on the corners of the nine interior subplots of each macroplot. During June immediately following logging, two subplots (sample plots) were selected at random within each macroplot. Within each sample plot all stumps and infested trees were tagged; species, infestation status, and diameter were recorded. For infested stumps, top diameter was measured to 0.1 cm. For trees, DBH was measured to the nearest 0.1 cm. Diameters of uninfested stumps were taken in Parson only. Five to ten randomly selected infested stumps (about 10–30% of all stumps) in each sample plot were sampled for attack by removing a strip of bark 15–30 cm wide from the top to mineral soil from the north side of each stump where attack density tends to be highest. No attacks originated below the duff–soil interface. As the sampling was destructive, sample size was kept to a minimum. The length and width of each bark sample were measured to the nearest 1 cm, and all adult beetles were placed in 70% ethanol and taken to the laboratory for identification. Collections were pooled by sample plot. Totals of 47, 46, and 40 stumps were sampled at Cranbrook, Elkford, and Parson, respectively. On attacked trees, the following information was recorded: number, size, and height above ground of logging scars; adjacency (within or outside 2 m) to skid trails; number of attacks (1–10, >10); attack success; and attacking bark beetle species. Attacks were judged unsuccessful if abandoned without egg laying or if parents and (or) eggs were killed by resinosis. All sample plots were resurveyed for new attack during June and August of subsequent years. In late September each year, all trees within the three sites were inspected for new attacks.

Analysis. Local species richness by area in stumps was estimated by (1) extrapolating species accumulation curves (Colwell and Coddington 1994), and (2) rarefaction (Heck

et al. 1975). In constructing the species accumulation curves, sample order was randomized 20 times and the mean and standard deviation of the number of species were computed and plotted over cumulative sample size (bark area). Species richness was extrapolated using the Michaelis–Menten equation (Colwell and Coddington 1994), the parameters of which were estimated by maximum likelihood. For comparison of species richness using rarefaction, the lowest number of beetles tallied in the three areas (Cranbrook) was designated as the "standard sample" (Magurran 1988). Margalef's index of diversity (Magurran 1988) was calculated for each area after rarefaction.

For the stump attack data, the logarithm of abundance was plotted *versus* species rank separately for each site. Based on examination of the resulting curves for linearity and steepness of slopes, the following abundance models were fitted to the data: the MacArthur broken stick model, the geometric series, and the Zeta distribution (Derman *et al.* 1973). This last distribution is also known as the Zipf–Mendelbrot model (Magurran 1988). Implicit assumptions underlying all of the fitted models are the total number of individuals is equivalent to the occupancy of the whole environment, and the species represent the niches (Southwood 1978). In addition, the MacArthur model assumes that niche boundaries are drawn at random. An additional assumption underlying the geometric model is that there is proportionate niche preemption by successively arriving species at regular time intervals. The Zeta distribution has its roots in econometrics and is not well known to biologists but has been applied widely to ranked-abundance data ranging from the size of cities to the distribution of genera by numbers of species. In the biological context this distribution arises when, in the sequence of arrivals to a particular resource, the probability that the next individual will be of species x is proportional to the size of population x that has arrived earlier. The ecological interpretation of the Zeta distribution is that it describes a successional process in which species colonize sites in some specific order. Later colonists, having more specific requirements, are consequently rarer than the first species to arrive (Frontier 1985). The rank abundances of species in some communities in which colonization of a resource is strongly affected by semiochemical communication may be described well by this distribution.

The Sorensen coefficient of similarity (C_s) was calculated for pairs of sites in all combinations to measure the extent to which species were common to the two habitats (Southwood 1978).

The data on the characteristics of infested trees and stumps and infestation incidence and severity in trees were analyzed by contingency χ^2 and analysis of variance with model factors for site and spacing treatment. When the analysis of variance for treatment effect was statistically significant, differences in means were tested by Tukey's test at the 5% probability level.

Results

Tree Species Composition and Logging Injury. In terms of initial stand density and average tree size as reflected in the control plots, the Elkford and Parson sites were more similar than the other combinations (Table 1). However, stand density in the spaced stands was uniform within each treatment. Average tree DBH and height were consistently higher in the spaced plots than in the controls because the larger (dominant, codominant) trees were retained. At the Cranbrook and Parson sites the overstorey was composed almost entirely of lodgepole pine, whereas at the Elkford site there was also a significant component (18.8%) of Engelmann spruce (Table 2).

The height of logging injury on the bole did not vary among sites ($F_{2,27} = 2.87$, $P > 0.05$). The mean height of injury at Elkford, Parson, and Cranbrook was 58.6, 96.5,

TABLE 3. Contingency table of the percentage of attacked trees by presence of logging injury (scar) and adjacency to skid trails (road) in spaced *Pinus contorta* stands during 1993–1996.

	No injury	Injury (scar)	Subtotal
Away from road	5.8	14.5	20.3
Adjacent to road	11.6	68.1	79.7
Subtotal	17.4	82.6	100.0

NOTE: Data are combined from the 4 × 4 m and 5 × 5 m spacing treatments and the three sites in British Columbia.

TABLE 4. Percentage of the total number of trees attacked by bark beetles by treatment and years following treatment (4 × 4 m and 5 × 5 m).

Year	Control	Combined spacing
1	27.3	73.1
2	45.4	19.2
3	27.3	7.7

NOTE: Data are combined from the three sites in British Columbia.

and 81.5 cm, respectively. Attacked trees were classified with respect to the presence or absence of logging injury and location, either within 2 m or greater than 2 m from skid trails (Table 3). There was no interaction between tree injury and adjacency to skid trails ($\chi^2_{[1]} = 1.69$, $P < 0.05$). However, there was deviation from an equal frequency among the four injury – road-adjacency classes (Table 3) ($\chi^2_{[4]} = 69.49$, $P < 0.001$). Over two-thirds of the attacked trees were located adjacent to skid trails and sustained injury from logging; 94.2% were injured and (or) were located adjacent to skid trails. The size of logging injury did not vary among sites ($F_{2,27} = 0.05$, $P > 0.05$). The mean size of logging injury was 253.4, 232.3, and 209.6 cm^2 for Elkford, Cranbrook, and Parson, respectively.

Characteristics and Density of Attacked Trees and Stumps. Sixty-seven trees were attacked by bark beetles during the first 3 years following spacing. All but one of the attacked trees were lodgepole pine, the sole exception being an Engelmann spruce in a control plot at Elkford. There were no differences among areas ($F_{2,4} = 1.04$, $P > 0.05$) or among treatments ($F_{2,4} = 1.80$, $P > 0.05$) in the number of trees attacked by secondary bark beetles. The mean number of attacked trees per subplot was 3.3, 6.0, and 1.8 for the 4 × 4 m spacing, 5 × 5 m spacing, and control treatments, respectively. Mean numbers of attacked trees per subplot for Cranbrook, Elkford, and Parson were 5.2, 2.0, and 4.0, respectively. There was interaction between the treatments and year following treatment in the number of attacked trees ($\chi^2_{[4]} = 8.70$, $P < 0.01$). The incidence of attacks declined with time in the spaced plots but not in the control plots (Table 4).

There was variation in stump height among sites ($F_{2,16} = 77.99$, $P < 0.001$), and all combinations of mean stump heights for the Elkford (28.6 cm), Parson (20.5 cm), and Cranbrook (16.2 cm) sites were different (Tukey's test, $P < 0.05$). The percentage of attacked stumps did not vary among sites ($F_{2,2} = 0.24$, $P > 0.05$) or among treatments ($F_{1,2} = 0.84$, $P > 0.05$); the overall mean was 80.7%. Attacks on stumps were affected by stump diameter ($F_{1,152} = 28.24$, $P < 0.0001$). Usually, unattacked stumps were of small size or the bark was damaged extensively by the harvesting operation. At the Parson site, where the diameters of both the attacked and unattacked stumps were measured, the mean diameters of unattacked stumps (16.0 and 19.5 cm for the 4 × 4 m and

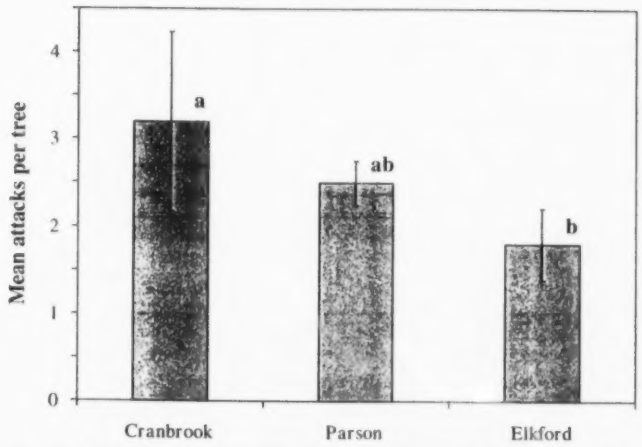

FIGURE 1. Mean (±SE) number of secondary bark beetle attacks per tree at three sites for the first 3 years following spacing treatment. Data are combined from the three spacing treatments. Means with the same letter are not significantly different (Tukey's test, $P > 0.05$).

5 × 5 m spacing treatments, respectively) were different (Tukey's test, $P < 0.05$) from the respective means for attacked stumps (20.1 and 25.6 cm).

Characteristics and Density of Bark Beetle Attacks on Trees. Of the 67 attacked trees, 15 (22.4%) were mass attacked and killed by one or more of the following species of Scolytidae: *Ips latidens* (LeConte), *Ips mexicanus* (Hopkins), *Ips pini* (Say), *Pityogenes knechteli* Swain, *Dendroctonus murrayanae* Hopkins, and *D. ponderosae*. Sixty percent of the trees killed were in control plots, including the only tree that succumbed to mountain pine beetle, a primary killer of lodgepole pine. The killed trees typically had small, thin crowns and were suppressed, or were suffering from wind damage (broken top, leaning). The attacks per tree varied among sites ($F_{2,143} = 5.16$, $P < 0.007$; Fig. 1) and among treatments ($F_{2,143} = 4.24$, $P < 0.05$; Fig. 2).

On trees that were only lightly attacked, 96.0% of the attacks at Cranbrook and 90.0% at Parson were made by *Dendroctonus valens* LeConte, whereas 70.0% of the attacks were made by *D. murrayanae* at Elkford. Attack success was different among spacing treatments ($\chi^2_{[2]} = 8.55$, $P < 0.05$; Fig. 3) but not among sites ($\chi^2_{[1]} = 3.67$, $P > 0.05$). Typically, trees attacked by *D. valens* or *D. murrayanae* were not killed or reattacked during the observation period. Most attacks were in the root collar region.

Bark Beetle Attack and Diversity in Stumps. Based on the sampling for adult scolytids boring in stumps during June and August following logging, there was variation in the density among sites ($F_{2,20} = 10.92$, $P < 0.05$) but not among treatments ($F_{1,20} = 0.91$, $P > 0.05$). The mean number of scolytids per square metre at Parson (480.52) differed from both Cranbrook (234.73) and Elkford (117.16), but there was no difference between the latter sites (Tukey's test, $P < 0.05$).

The species accumulation curves for all three sites approached their respective asymptotes (Fig. 4), indicating that sample sizes were adequate for determination of species richness. The observed number of species ranged from 76 to 90% of those estimated (S_{max}, Table 5).

The estimated species richness of bark beetles attacking stumps at Cranbrook, Elkford, and Parson was 9.21, 7.44, and 10.02, respectively (S_{max} in Table 5). The

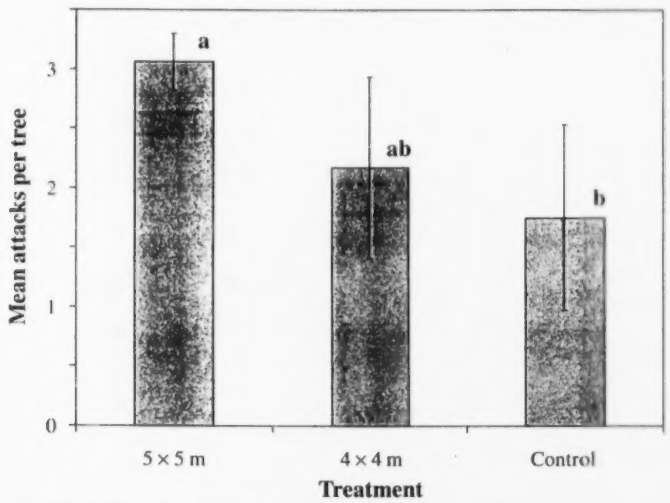

FIGURE 2. Mean (±SE) number of secondary bark beetle attacks per tree by treatment for the first 3 years following spacing. Data are combined from the three sites. Means with the same letter are not significantly different (Tukey's test, $P > 0.05$).

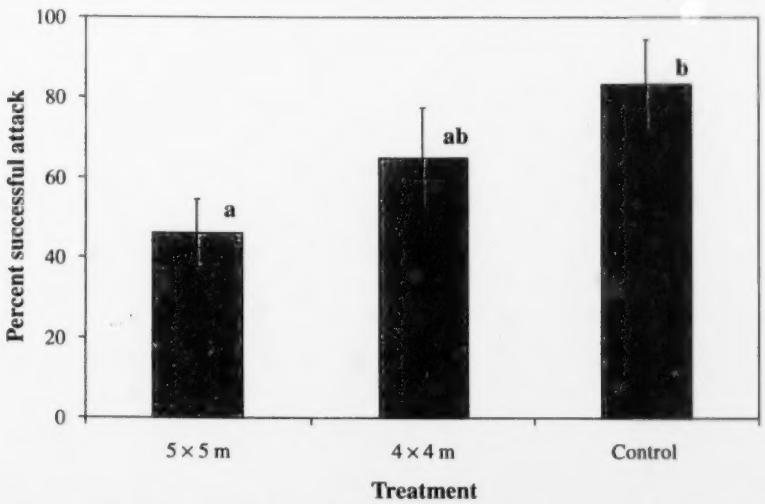

FIGURE 3. Mean (±SE) percentage of successful bark beetles attacks by treatment for the first 3 years following spacing. Data are combined for the three sites. Means with the same letter are not significantly different (Tukey's test, $P > 0.05$).

corresponding Margalef diversity indices, based on rarefaction, were 1.15, 0.89, and 1.13 (Table 5). Hence, both species richness and diversity were more similar at the drier (Cranbrook and Parson) sites than at the wetter (Elkford) site.

Plots of the logarithm of abundance *versus* species rank and the abundance *versus* the logarithm of species rank relationships were both inversely J-shaped, especially for the Cranbrook and Parson data, but log–log plots of these variables were approximately

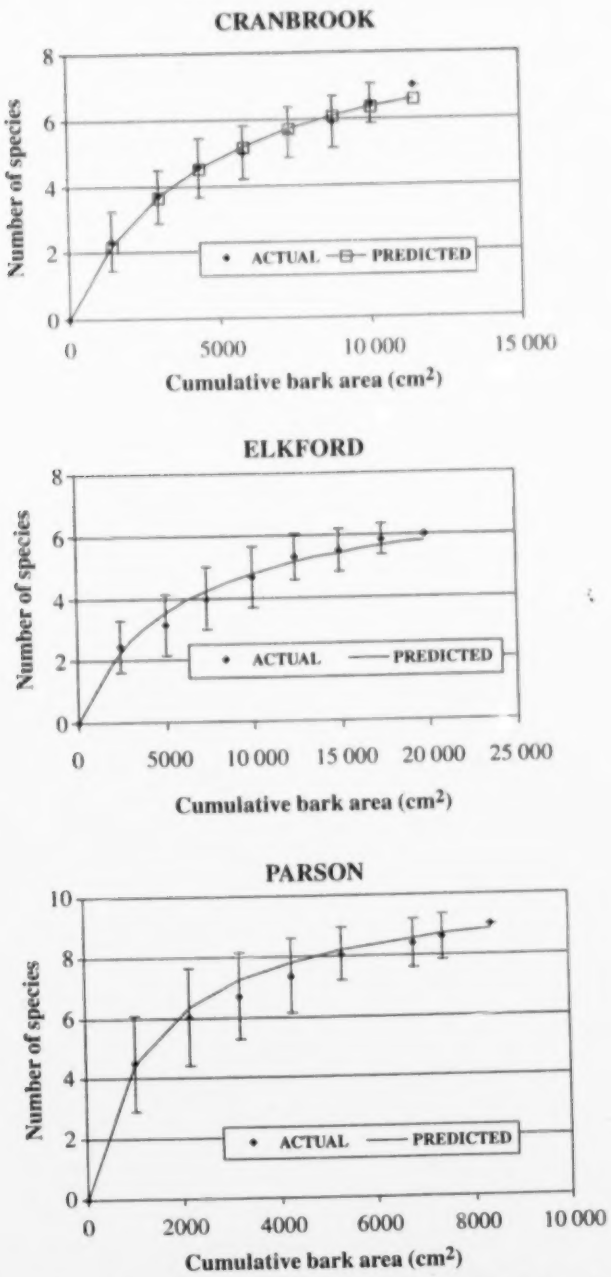

FIGURE 4. Species accumulation curves of bark beetles attacking stumps for three sites. Each point represents the mean (±SE) of 20 randomizations of bark sample pooling order. The solid lines represent the fitted Michaelis–Menten equation (estimated parameters are given in Table 5).

TABLE 5. Number of bark beetles (N), estimated number of species attacking stumps after rarefaction (S), parameters of the Michaelis–Menten equation (S_{max}, B), and Margalef's index of diversity (M_d) at three sites in British Columbia.

Site	N	S	S_{max}	B	M_d
Cranbrook	185	7.00	9.21	4514.35	1.15
Elkford	208	5.63	7.44	5574.32	0.89
Parson	378	6.91	10.02	1315.32	1.13

NOTE: The standard sample for the rarefaction calculation was the Cranbrook data (N = 185). $S = (S_{max}) \times$ (sample area) / (B + sample area), where sample area is the size of the bark sample (cm^2); S_{max} is the estimated number of species at a site; and B is the estimated constant. $M_d = (S - 1) / \ln N$.

linear. This indicated that the geometric series or the Zeta distribution may give satisfactory fit to the data. Of the three models tested, the MacArthur model gave the poorest fit to the abundance *versus* species rank relationship at all three sites (Table 6). At Cranbrook and Parson, the Zeta distribution gave a better fit to the data than the geometric model ($\chi^2_{[5]} = 3.31$ and 4.98, $P > 0.05$). At Parson, none of the fitted models gave a satisfactory fit to the data, mainly due to the high abundance of the second ranked species (*Orthotomicus caelatus* Eichhoff). At Parson, even the occurrences of the rarer species were better described by the Zeta distribution than by the other two models. The alpha coefficient of the Zeta distribution was nearly identical for the three sites and ranged from 1.55 to 1.60.

Twelve species of bark beetles were found attacking stumps at the three sites (Table 6). Only four species were common to all sites and 5, 5, and 6 species were common to the Cranbrook–Elkford, Cranbrook–Parson, and Elkford–Parson paired sites, respectively. The corresponding Sorensen coefficients of similarity (C_s) were 0.62, 0.53, and 0.71, indicating that the Elkford–Parson pair was more similar in species composition than the other combinations. *Hylurgops porosus* was the most numerous species attacking stumps at all three sites.

Trypodendron lineatum (Olivier) was found in all areas, but the data were excluded from the models because this insect breeds in the wood rather than in the inner bark as do the balance of the recorded species.

Discussion

The method of harvesting did not have a significant effect on the average height of injury among sites. Skidding followed hand felling at Elkford, whereas feller-bunchers were used at Cranbrook and Parson. The average heights of injury on attacked trees at Elkford (58.6 cm) and Cranbrook (81.5 cm) were lower than the corresponding values of 70.5 and 103.5 cm for all injured trees (attacked plus unattacked) published in Mitchell (1994). Most of the attacks were made by *D. murrayanae* and *D. valens*. Both species prefer to attack near the ground in the root collar region and are strongly attracted to trees with fresh basal injuries (Wood 1982).

Single injuries were most common, and multiple injuries were found most often along skid trails. The average number of 1.6 injuries per attacked-plus-injured tree compares favourably with the corresponding average of 1.7 for all injured trees for Elkford and Cranbrook (Mitchell 1994). Although fresh harvesting injuries predisposed trees to bark beetle attack, the dominant predisposing factor was the combination of harvesting injury and adjacency to skid trails; over two-thirds of the attacked trees fell into this category. Many trees located adjacent to skid trails probably sustained some injury to

TABLE 6. Fitting three diversity models to ranked abundance of bark beetle species attacking stumps in spaced *Pinus contorta* at three sites in British Columbia.

Species	Abundance	Model 1*	Model 2†	Model 3‡
		Cranbrook		
Hylurgops porosus	145	68	99	144
Hylastes nigrinus	19	42	46	24
Dendroctonus valens	12	29	22	8
Pityogenes knechteli	4	20	10	4
Ips pini	3	13	5	2
Ips latidens	1	8	2	1
Orthotomicus caelatus	1	4	1	1
		Elkford		
Hylurgops porosus	160	85	117	163
Dendroctonus murrayanae	35	50	52	27
Dendroctonus valens	5	33	23	9
Pityogenes knechteli	4	21	10	4
Ips pini	2	13	4	2
Hylurgops rugipennis	2	6	2	2
		Parson		
Hylurgops porosus	232	116	181	290
Orthotomicus caelatus	108	75	95	50
Hylurgops reticulatus	13	54	49	18
Hylurgops rugipennis	11	41	26	8
Ips mexicanus	8	30	13	5
Dendroctonus valens	3	22	7	3
Dendroctonus murrayanae	1	15	4	2
Dryocoetes autographus	1	10	2	1
Ips pini	1	5	1	1

NOTE: the estimated counts were rounded to the nearest integer.

*MacArthur broken stick: $N_i/S_t \sum_{n=i}^{S_t} (1/n)$, where N_i is the expected number of individuals of the ith ranked species, N_t is the total number of insects, S_t is the total number of species, and n is the species rank.

†Geometric series: $N_i = N_t Cp(1-p)^{(i-1)}$, where p is the proportion of the available resource that each species occupies (0.535, 0.556, and 0.478 for the Cranbrook, Elkford, and Parson sites, respectively); $C = [1-(1-p)^{S_t}]^{-1}$; and i is the species rank. P values were estimated from the iterative solution of the following equation: $N_{min}/N = [k/(1-k)](1-k)^{S_t-1}/[1-(1-k)^{S_t-1}]$ (Magurran 1988).

‡Zeta distribution: $N_i = N_t Ci^{(\alpha+1)}$, where N_t, N_i, and i are as defined above; C is a constant (0.776, 0.785, and 0.764 for the Cranbrook, Elkford, and Parson sites, respectively); and α is a constant (1.57, 1.60, and 1.55 for the Cranbrook, Elkford, and Parson sites, respectively).

their root systems through trampling and soil compaction by the harvesting equipment. Such trees may have become susceptible to attack from *D. valens* and *D. murrayanae* but had no visible evidence of injury to the bole.

The total number of trees attacked in the spaced subplots at Cranbrook, Elkford, and Parson represents 10.3, 0.8, and 1.9% of the residual trees, respectively. The numbers of trees attacked per subplot did not differ among the three sites, although the Cranbrook site had a substantially higher incidence of attack. There, one of the 5 × 5 m subplots was susceptible to soil saturation and wind damage, and sustained an attack incidence of 25.0%.

Mass-attacked trees typically had poor crowns or were heavily damaged by wind or the harvesting operation. Lightly attacked trees survived, but with some phloem necrosis. On trees sustaining up to 10 attacks, there was a direct relationship between attack success and residual tree density. This implies that for *D. valens* and *D. murrayanae*, host density is an important factor that affects attack behaviour through changes in microclimate or the characteristics of *in situ* resin in the inner bark. The two drier sites at the lower elevations (Cranbrook and Parson) supported mainly *D. valens* populations, whereas the wetter and higher elevation site supported mainly *D. murrayanae*.

These observations show the importance of minimizing the number of skid trails and preventing bark damage on the residual trees in spacing and thinning operations. Such damage leaves the trees susceptible to attack by secondary beetle species and provides arenas for disease invasions, which are seldom fatal but may cause growth loss and (or) predisposition to attack by the mountain pine beetle.

The species accumulation curves (Fig. 4) indicated that for assessment of species richness in stumps of selectively logged, lodgepole-pine-dominated mature stands, it is necessary to sample at least 50 stumps and remove a total of 1–1.5 m^2 of bark. In our study, the 40–47 sampled stumps per site, representing a range of 0.8–2.0 m^2 total sampled bark area, yielded 76–90% of the estimated number of species based on the Michaelis–Menten equation (Table 5). Most of the fresh stumps were colonized by bark beetles. Of the 12 Scolytidae found in stumps at the three sites, five species, namely *Dryocoetes autographus* (Ratzeburg), *Hylastes nigrinus* (Mannerheim), *Hylurgops porosus* LeConte, *Hylurgops reticulatus* Wood, and *Hylurgops rugipennis* (Mannerheim), are attracted to souring sap of the host and readily attack fresh stumps. Attacks on stumps by species of *Hylurgops* and *Hylastes* are usually below or near the duff line. Of this group, *H. porosus* breeds extensively in the roots. Owing to the commercial harvesting operations and natural tree mortality in mature stands, this resource is normally highly abundant and maintains high *H. porosus* populations. *Dendroctonus valens* and *D. murrayanae* are attracted by resin volatiles from injured or freshly killed hosts. Both species commonly attack fresh stumps. Attacks by these species normally occur above duff, near the duff line. The *Ips* species (*I. mexicanus*, *I. latidens*, *I. pini*) and *P. knechteli* normally attack injured, diseased, dying, or decadent trees, or trees killed by more aggressive bark beetles such as the mountain pine beetle. They are repelled by resin production and normally breed in the thin-barked portions of the bole rather than in stumps. For this reason, stumps would normally be attacked after resin production had ceased. *Orthotomicus caelatus* has host requirements similar to those of the *Ips* species except that it normally breeds in the thicker barked section of the bole and frequently attacks stumps (Keen 1952; Bright 1976). Hence the subcortical habitat of stumps is colonized by various bark beetle species based on a combination of preferences for a particular host condition or part. Host-finding and attack behaviour are mediated through chemical signals from the host and semiochemical communication within and between species.

Of the 12 species of secondary bark beetles that infest the root collar region, the roots of fresh stumps or unthrifty or freshly killed pines in southern British Columbia (Bright 1976; Furniss and Carolyn 1977), eight species were recorded attacking stumps in the three sites. The four species not recorded by us were *Hylastes gracilis* LeConte, *Hylastes macer* LeConte, *Hylastes longicollis* Swaine, and *Hylastes tenuis* (Eichoff). The biology of these species has not been investigated. Their absence in our samples may have been due to low abundance, because lodgepole pine is not a major host. Only *H. longicollis* has been recorded from lodgepole pine (Bright 1976). The balance of the

bark beetle species we found (*Ips* spp. and *P. knechteli*) generally prefer thin bark and normally do not breed in stumps.

Although the dominant tree cover on all three sites was lodgepole pine (Table 2), the sites represented different ecological units as described above. These differences were reflected by the bark beetle species assemblages and relative abundance in stumps. Estimating species richness by rarefaction, and using the Michaelis–Menten equation, indicated that the two drier sites, Cranbrook and Parson, were more similar than the other site combinations. The observed difference in the number of bark beetle species at Cranbrook and Parson was therefore mainly due to the difference in sample size. In addition to being the wettest site, Elkford had a smaller percentage of lodgepole pine (Table 2) than the other two sites. As the main hosts of the observed bark beetle species collected from stumps are pine, the wetter climate and (consequent) reduced lodgepole pine component are the probable main reasons for the reduced bark beetle species richness at this site. Although the Sorensen coefficient of similarity indicated that the Elkford–Parson pair was more similar than the other combinations, the coefficients for all combinations of site pairs were rather low. The reliability of this coefficient is influenced by the completeness of species lists. Because only an estimated 76–90% of the bark beetle species attacking stumps at the three sites were found in the samples, a much larger sample size would be required for a reliable assessment of the similarity of species complexes among sites.

Based on the foregoing discussion regarding host preference and attack behaviour, the assumption of randomness of niche boundaries in the MacArthur model appears unrealistic for bark beetles breeding in stumps. A stump is a nonuniform resource with respect to colonization by bark beetles. The attacking beetles partition the total bark area of a stump by their species' preference, although niches will overlap. For example, *I. latidens* do not attack roots; their attack is mainly confined to the thin-barked areas near the tops of stumps, and may overlap attacks by other species of *Ips* and *P. knechteli*. The broken-stick model would apply if the resource were shared more or less evenly among species (Magurran 1988), which explains its poor fit to our data. The geometric series pattern of abundance occurs mainly in species-poor habitats or at early stages of succession (Whittaker 1965). As bark beetles are the first insects to colonize fresh stumps, this model would appear to fit the ecological nature of the problem. As all of the bark beetle species recorded from stumps attack more or less simultaneously in the spring, they all search for suitable attack sites during the same time period. The assumptions of the geometric model also fail to match the biological process of host colonization because (*i*) not all attack sites are available to all species, and those that are available are not equally suitable; and (*ii*) interspecific and intraspecific communication play an important role in resource partitioning. The Zeta distribution gave a better fit to the rank-abundance data than the geometric series mainly because (*i*) high populations of *H. porosus* were present at all three sites and it breeds extensively in roots; (*ii*) the bark area of roots on stumps is normally the major breeding resource for bark beetles; and (*iii*) attacks by species of *Ips* and of *Pityogenes*, having special requirements, were confined to thinner-barked areas and were generally less common than attacks by species that preferred the roots and the root collar region.

Of the bark beetle complex breeding in stumps at the tree sites, *D. murrayanae*, *D. valens*, and *I. pini* are attracted to and kill injured or unthrifty trees. Trees attacked by *I. pini* can also serve as suitable habitat for maintaining low population levels of the mountain pine beetle. Some species of *Hylastes* kill young seedlings by feeding on the bark at the base of the stem. It is therefore important during spacing and thinning operations that tree injuries be kept to a minimum, that stumps be cut as low as possible, and that the operation be carried out during the winter to reduce soil disturbance and root trampling. Trees should be extracted whole and bucked at landings. Any slash left in

the stand should be scattered to accelerate drying. Slash burning within the stand should be avoided to prevent scorching of the residual trees. More detailed and complete guidelines for reducing bark beetle hazard following thinning operations are given in Safranyik and Morrison (1998).

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References

Amman GD. 1989. Why partial cutting in lodgepole pine stands reduces losses to mountain pine beetle. pp. 48–59 *in* GD Amman (Compiler), Proceedings of a Symposium on the Management of Lodgepole Pine to Minimize Losses to the Mountain Pine Beetle, 12–14 July 1988, Kalispell, Montana. *U.S. Forest Service General Technical Report* **INT-262**

Braumandl TF, Curran MP (compilers). 1992. A field guide for site identification and interpretation for the Nelson Forest Region. *British Columbia Ministry of Forests Land Management Handbook* **20**

Bright DE, Jr. 1976. The bark beetles of Canada and Alaska. Coleoptera: Scolytidae. *Canada Department of Agriculture, Biosystematic Research Institute, Research Branch Publication* **1526**

Cole DM, McGregor MD. 1985. Silvicultural practices for lodgepole pine stands in commercial forests. pp. 47–56 *in* MD McGregor, DM Cole (Eds.), Integrating management strategies for the mountain pine beetle with multiple-resource management of lodgepole pine forests. *U.S. Forest Service General Technical Report* **INT-174**

Colwell RK, Coddington JA. 1994. Estimating territorial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London* **345**: 101–18

Derman C, Gleser LJ, Olkin I. 1973. *A Guide to Probability Theory and Application.* New York: Holt, Reinhart and Wilson, Inc.

Frontier S. 1985. Diversity and structure in aquatic ecosystems. pp. 253–312 *in* M Barnes (Ed.), *Oceanography and Marine Biology, Annual Review.* Aberdeen: Aberdeen University Press

Furniss RL, Carolyn VM. 1977. Western forest insects. *U.S. Department of Agriculture Miscellaneous Publication* **1339**

Heck KL, van Belle G, Siberloff D. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology* **56**:1459–61

Keen FP. 1952. Insect enemies of western forests. *U.S. Department of Agriculture, Miscellaneous Publication* **273**

Magurran AE. 1988. *Ecological Diversity and its Measurement.* Princeton: Princeton University Press

Mitchell JL. 1994. Commercial thinning of mature lodgepole pine to reduce susceptibility to mountain pine beetle. *Canadian Forestry Service, Pacific Forestry Centre, FRDA Report* **224**

Mitchell RG, Waring RH, Pitman GB. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science* **29**: 204–11

Ramsey CB (editor). 1998. Stand Density Management: Planning and Implementation, Conference Proceedings, 6–7 Nov. 1997, Edmonton

Safranyik L, Morrison D. 1998. Stand protection issues in thinning. pp. 84–91 *in* CR Ramsey (Ed.), Stand Density Management: Planning and Implementation, Conference Proceedings, 6–7 Nov. 1997, Edmonton

Southwood TRE. 1978. *Ecological Methods.* 2nd ed. New York: Chapman and Hall

Waring RH, Pitman GB. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* **66**: 889–97

Whittaker RH. 1965. Dominance and diversity in land plant communities. *Science* (*Washington, D.C.*) **147**: 250–60

Wood SL. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs* **6**

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